

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

**Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects**

**This is the author's manuscript**

*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/1666685> since 2018-04-19T12:51:48Z

*Published version:*

DOI:10.1016/j.biocon.2018.03.008

*Terms of use:*

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)



# UNIVERSITÀ DEGLI STUDI DI TORINO

***This is an author version of the contribution published on:***

*Questa è la versione dell'autore dell'opera:*

*[**Biological Conservation**, 221: 209-218, 2018, DOI: [10.1016/j.biocon.2018.03.008](https://doi.org/10.1016/j.biocon.2018.03.008)]*

***The definitive version is available at:***

*La versione definitiva è disponibile alla URL:*

*<https://www.sciencedirect.com/science/article/pii/S0006320717319109>*

# **Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: management options to buffer against global warming effects**

Mattia Brambilla<sup>\*a,b</sup>, Jaime Resano-Mayor<sup>\*c</sup>, Davide Scridel<sup>\*a,d</sup>, Matteo Anderle<sup>a</sup>, Giuseppe Bogliani<sup>d</sup>, Veronika Braunisch<sup>c</sup>, Federico Capelli<sup>a,e</sup>, Matteo Cortesi<sup>a,e</sup>, Nathan Horrenberger<sup>c</sup>, Paolo Pedrini<sup>a</sup>, Beatrice Sangalli<sup>c</sup>, Dan Chamberlain<sup>f</sup>, Raphaël Arlettaz<sup>c</sup>, Diego Rubolini<sup>c</sup>

<sup>\*</sup>shared first-authors

<sup>a</sup> Museo delle Scienze, Sezione Zoologia dei Vertebrati, Corso della Scienza e del Lavoro 3, I-38123 Trento, Italy

<sup>b</sup> Fondazione Lombardia per l'Ambiente, Settore Biodiversità e Aree protette, Largo 10 luglio 1976 1, I-20822 Seveso, MB, Italy

<sup>c</sup> University of Bern, Institute of Ecology and Evolution, Division of Conservation Biology, Baltzerstrasse 6, CH-3012 Bern, Switzerland

<sup>d</sup> Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, Pavia, Italy

<sup>e</sup> Dipartimento di Bioscienze, Università degli Studi di Milano, Via Celoria 26, 20133 Milan, Italy

<sup>f</sup> Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123, Turin, Italy

Corresponding author: Mattia Brambilla, email: [brambilla.mattia@gmail.com](mailto:brambilla.mattia@gmail.com)

## Abstract

The majority of predictions about the impacts of climate change on wildlife have relied either on the study of species' physiological tolerance or on broad-scale distribution models. In comparison, little attention has been paid to species' mechanistic responses to fine-grained, climate-induced modifications of habitat suitability. However, such studies would be pivotal to the understanding of species' ecological requirements, and hence their adaptive potential to environmental change which can act as a basis for designing management strategies. We investigated foraging microhabitat selection in a climate-change endangered, high-elevation bird species, the white-winged snowfinch *Montifringilla nivalis*, during the breeding season in the European Alps. Our microhabitat selection model considered various topographical and ground cover variables, as well as sward height, comparing environmental characteristics within a 5-m radius at foraging and random locations, the latter serving as controls. Foraging habitat selection of *M. nivalis* was positively affected by grassland cover but negatively by sward height. The response to snow cover was quadratic, with an optimum around 40%; the birds also avoided anthropized (urban areas, roads) sites. We estimated past (1976) and future (2066) climate-driven changes in foraging microhabitat suitability, assuming a progressively earlier date of snowmelt due to increasing temperatures over this entire time span. We then modelled the potential impact of snow-melt (and related sward height) on habitat suitability under two scenarios: maintaining the current situation (i.e. some seasonal grazing) and implementing targeted management (e.g. grazing) in an attempt to mitigate impacts of earlier snowmelt. Predicted foraging habitat suitability (estimated as the fraction of suitable plots) significantly declined over time, with a 23% reduction in the number of suitable plots between 1976 and 2016, and a further 32% loss by 2066. However, model outputs demonstrated that maintaining sward height below 6 cm on breeding grounds (e.g. by grazing) would significantly decrease the predicted loss of suitable foraging habitat. Our study shows that detailed information about patterns of resource exploitation not only allows the identification of mechanistic, functional responses of

species to environmental change, but also enables an evaluation of habitat options that can buffer against the detrimental effects of global warming.

## **Keywords**

Alps – habitat selection – microhabitat – mitigation – *Montifringilla nivalis* – snow cover – snowmelt

## Introduction

Anthropogenic climate change is increasingly threatening ecosystems and species worldwide (IPCC, 2013; Rosenzweig et al., 2008). Evidence from a wide range of taxa and ecological systems suggests that climate change has already started to affect biodiversity at a global scale (e.g. Carnaval and Moritz, 2008), for instance by modifying species distributions, altering their habitats or increasing extinction risk due to rapid shifts in abiotic conditions (Chen et al., 2011; Parmesan and Yohe, 2003). Based on forecast climatic scenarios, several studies have furthermore attempted to predict future climatic impacts on biodiversity (e.g. Bellard et al., 2012; Thomas et al., 2004).

The potential effects of climate, and hence of climate change, on animal species have been mostly assessed either by experimental approaches evaluating physiological tolerance to climate variations (e.g. temperature) at the individual level (Johnson, 1968) and under controlled environments (Chapin et al., 1995), or via large-scale distribution models, the latter representing one of the commonest ways to explore potential changes in species distributions owing to climate change (Fitzpatrick and Hargrove, 2009; Hijmans and Graham, 2006). Eco-physiological investigations usually include field observations and laboratory measurements that aim to detect how alterations of environmental constraints influence species' physiological responses and hence population processes (Arlettaz et al., 2000; Pörtner and Knust, 2007). In contrast, correlative models of species distribution (Guisan and Thuiller, 2005) rely on environmental factors such as climate, land-cover and topographical variables, which are usually linked with species occurrence at a broad scale. They can, to a certain extent, be downscaled to the territory/home-range size of a target species (Brambilla et al., 2015; Braunisch et al., 2013), but often remain fairly crude in their predictive power as they may miss essential mechanistic components (Williams and Jackson, 2007) linked to patterns of resources exploitation, such as food acquisition, i.e. they may not embrace species' niche complexity as a whole (Brambilla et al., 2015; Braunisch et al., 2013). Despite this

serious caveat, species distribution models remain the most used (and scalable) and widespread approach to assess species' spatio-temporal responses to climate change (Moritz and Agudo, 2013). Correlative in essence, such models may both over- and underestimate extinction risk due to climate change (Bellard et al., 2012). There is therefore a need for complementary approaches that integrate finer-scale ecological information for, on the one hand, improving our mechanistic understanding of the tolerance and resilience, i.e. adaptive potential of target organisms to shifting environmental conditions (e.g. Baudier et al., 2015; Bennett et al., 2015), and, on the other hand, modelling appropriately the consequences of environmental changes upon population dynamics (e.g. Fedy and Martin, 2011). This could be addressed by considering the impacts of climate change upon fine-scale habitat structure and availability (henceforth, microhabitat), which eventually drives habitat suitability. However, this aspect has received comparatively very little attention so far, despite its crucial importance in understanding mechanistic responses of species to environmental change, in particular their adaptive potential, for more accurate forecasts. Fine-grained species-habitat associations are essential to understand how changes in microhabitat due to climate change will affect species' habitat suitability at local and broader scales, which will ultimately influence a species' ability to respond to climate-induced environmental changes (Scheffers et al., 2014).

Studies of the effects of microhabitat alteration due to changing climatic conditions have mostly focused on small-sized organisms (e.g. invertebrates) that are very sensitive to local climatic/habitat variation, especially due to their strong temperature-dependent life-cycles (Davies et al., 2006). Pincebourde et al. (2016) have shown that microhabitat properties shape species responses to climate change. Research has generally focused on species with limited mobility (e.g. plants (Pradervand et al., 2014), benthic invertebrates (Schiel et al., 2004)). In contrast, studies on the distribution of terrestrial and highly-mobile species usually deal with broad spatial scales, despite the fact that habitat selection in these species operates at multiple scales. In birds for instance, this concerns the selection of breeding sites (Jedlikowski et al., 2016; Rauter et al., 2002),

foraging grounds (Brambilla et al., 2017b; Martínez-Miranzo et al., 2016; Schaub et al., 2010), and even shelters to avoid unsuitable climate (Visinoni et al., 2015). An absence of information about microhabitat preferences can lead to serious biases in predictions of climate change effects on species distributions (cf. Bellard et al., 2012). As a matter of fact, microhabitat characteristics may allow species persistence when the general climate of the region appears to have become unsuitable, and vice versa. Studies of microhabitat suitability are thus pivotal to our basic understanding of species' ecological requirements and to efficient conservation management of climate-sensitive biodiversity. Several such studies have emerged recently (Suggitt et al., 2011; Turlure et al., 2010), which have established the importance of both microhabitat and microclimate to understand the sensitivity of species to environmental shifts and, ultimately, their population dynamics and distribution patterns (Fedy and Martin, 2011; Frey et al., 2016). The basic question here is to which extent can microhabitat characteristics and potential management thereof buffer against any detrimental effects of overall climate change (e.g. Braunisch et al., 2014)?

Among terrestrial organisms, high-elevation cold-adapted species seem to be particularly vulnerable to climate change (Dirnböck et al., 2011; Lagerholm et al., 2017), with their future distribution being either expected to contract towards higher elevations due to ambient temperature warming (La Sorte and Jetz, 2010; Braunisch et al., 2013; Chamberlain et al., 2013; Pernollet et al., 2015; Sekercioglu et al., 2008), or to vary in a complex way in response to shifts in precipitation regimes that remain difficult to forecast (e.g. Tingley et al., 2012). Mountain areas are indeed subject to higher rates of warming compared to the global average (e.g. Böhm et al., 2001; Brunetti et al., 2009), yet at the same time, they are also experiencing strong changes in landscape and land use (e.g. forest encroachment in abandoned pastures, upward treeline shift or loss of areas permanently covered by snow). High-elevation ecosystems thus represent an ideal setting to investigate the fine-grained impact of environmental change on habitat and biocenoses, especially due to the complex topography, including steep altitudinal gradients, that generates a large range of



microhabitats and microclimates (hereafter topoclimates) and offers numerous refugia opportunities (Körner and Ohsawa, 2006). Such heterogeneity may *per se* represent a chance to maintain biodiversity, either naturally (Brambilla et al., 2016b) or through informed conservation management (Braunisch et al., 2014). However, to the best of our knowledge, mitigation strategies to maintain niche opportunities for high-alpine biodiversity facing climatic risks have never been investigated so far (Shoo et al., 2011; Turlure et al., 2010).

In this study, we investigated the foraging microhabitat selection in a high-elevation, cold-adapted passerine bird, the white-winged snowfinch *Montifringilla nivalis* (Aves: Passeridae; henceforth: snowfinch), during the nestling rearing period, a crucial phase of the life-cycle – especially for short-lived species such as the snowfinch – which is likely to drive overall population dynamics (Hanssen et al., 2005). We first identified key habitat characteristics that influence site selection for food collection by parents and current habitat suitability in the Central Alps. As snow cover appears crucial (Brambilla et al., 2017b; this study), we then constructed past and future distribution models based on longitudinal data (both historical and projected) on the timing of snowmelt, exploring recent past and future variation in foraging habitat suitability in parts of the Italian and Swiss Alps. More specifically, our aims were: 1) to identify key habitat factors driving foraging microhabitat selection during food provisioning to chicks by parents; 2) to evaluate past and forecast future changes in foraging microhabitat suitability in relation to changing climatic conditions (snowmelt date; (Klein et al., 2016); and, 3) to assess whether habitat management operations could maintain microhabitat suitability in the face of climate change. To the best of our knowledge, this is the first study to explicitly model the potential impact of climate change on foraging microhabitat suitability in a terrestrial vertebrate, which paves the way for better forecasts of wildlife responses to climate-induced alterations of habitat, and provides targeted conservation guidance for maintaining suitable foraging grounds in the face of climate change.

## **Methods**

### **Study species**

The snowfinch is a mountain specialist bird breeding at high elevations above the treeline (in the European Alps mostly between 1800 and 3000 m asl; Cramp and Perrins, 1994). Nests are usually located in rock crevices or human-built infrastructure such as mountain buildings or ski-lift pylons (Cramp and Perrins, 1994), where at the end of May-early June snowfinches lay 4-5 eggs. After two weeks of incubation performed exclusively by the female, hatching occurs and nestlings fledge at ca. 18-22 days of age (del Hoyo et al. 2009). During the nestling rearing period, adults collect invertebrate prey in the proximity of nest sites, usually within 300 m of the nest, frequently on or at the margin of melting snow patches and in alpine grasslands (Antor, 1995; Brambilla et al., 2017b; Catzefflis, 1975; Cramp and Perrins, 1994; Strinella et al., 2007).

A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower values favoured, especially late in the season, indicating avoidance of warmer sites). That study was based on 314 m<sup>2</sup> plots (i.e. at meso-scale) and did not explicitly address the key question of climate change effects on habitat suitability (Brambilla et al., 2017b). Based on the outcome of correlative distribution models which accounted for climatic, topographic and land-cover variables (both at the landscape (Maggini et al., 2014) and the territory level (Brambilla et al., 2016b), the snowfinch is expected to undergo a marked range contraction in the Alps because of climate change, and especially due to ambient temperature increase and habitat loss, snow cover being a key component in the species' ecology (Brambilla et al., 2017b). Our objectives were to quantifying the magnitude of foraging habitat loss, and to identify habitat management measures that might help mitigate any detrimental effects.

## **Study area and data collection**

We investigated foraging microhabitat selection by snowfinches breeding at 12 breeding sites in 8 different regions (Sorebois, Zermatt, Furka Pass, Valle Spluga, Stelvio, Gavia, Passo Sella, Rosetta) in the Swiss and Italian Alps (Fig. 1). The elevation of the study sites ranged from 1880 to 2840 m a.s.l., adequately covering the altitudinal and macroclimatic gradient of snowfinch distribution in the Alps. All surveys were carried out between 14<sup>th</sup> June and 26<sup>th</sup> July 2016, focusing exclusively on snowfinches collecting food for nestlings (nestling-rearing period). First, by means of direct observations, we located snowfinch breeding pairs and active nests. Once an occupied nest was located, we adopted the following field protocols in order to record foraging and random non-foraging points (hereafter, foraging and control plots).

In Switzerland, we mist-netted at least one parent from each monitored breeding pair to attach a radio-transmitter (Holohil Systems Ltd., model BD-2, weight: 1.4 g – corresponding to 3.2-3.9% of our birds' body mass, life span: 9 weeks) to its back using a leg-loop harness (Naef-Daenzer et al., 2001; Rappole and Tipton, 1991). Studies of the effects of radio-transmitters on passerines have shown no negative impact on physiology, behaviour or survival (Naef-Daenzer et al., 2001; Townsend et al., 2012) as long as tag weight is less than 5% of bird body mass. As soon as tagged birds were provisioning food to the nestlings, foraging events were monitored over 2-6 days with the aid of a hand-held three-element foldable Yagi antenna wired to a radio-receiver (Australis 26k, Lawnton, Australia). Radio-tagged birds were first located from a distance from the radio signal and, once the foraging bird was visually located, the exact site of a successful prey capture was located with the aid of binoculars and marked with a labelled stick. Then, a control plot was generated by selecting a random angle (0-359°) and a random distance (between 26-100 m) from the actual foraging plot.

In Italy, breeding individuals were visually tracked when flying from the nest to foraging sites, with the help of binoculars (Brambilla et al., 2017b). Once a foraging event was encountered, the exact location was recorded with a GPS device or by mapping the point on a detailed aerial photograph. The foraging location was established as the first position where a food item was collected (or as the last location of the bird before returning to the nest, when we could not directly assess prey capture, since snowfinches usually provision food to the nest immediately after prey capture; Brambilla et al., 2017b). After the collection of 10 foraging locations per study pair, an equal number of control plots were randomly selected within a radius of 300 m around the nest (Brambilla et al., 2017b; Grangé, 2008; Strinella et al., 2007) so as to map habitat characteristics.

Habitat cover and structure were recorded within a 5 m-radius around each foraging location and control plot. Habitat variables described vegetation and other ground cover, as well as sward height and the occurrence of grazing (Table 1). In addition, topographical features (slope, solar radiation) were calculated in a geographic information system (GRASS 7.04) using detailed Digital Elevation Models (resolution between 1 and 5 m) made publicly available by regional/provincial authorities in Italy and by SwissTopo maps for 2013 (Swiss Federal Office of Topography). Solar radiation was calculated as global radiation on 21<sup>st</sup> June, taking into account the shadowing effect of the relief.

Sward height was obviously not recorded where grass was absent (N = 16 locations out of a total of 470). Due to this absence, in exploratory analyses we compared the modelled relationships between foraging occurrence and sward height by setting sward height to zero at these 16 locations against omitting them from the analysis. Given that the coefficients for sward height were very similar between models with and without ‘filled gaps’ (-1.02 and -1.03, respectively), we considered it appropriate to apply the former option.

## **Statistical analyses**

### **Foraging habitat selection**

Habitat variables were recorded at 470 locations (235 foraging and 235 control plots) obtained from 22 breeding pairs. All variables were standardized (i.e. centred on their mean and scaled by their standard deviation SD) prior to analyses. After checking for outliers and zero-inflated variables, sand and mud cover were discarded, and human-altered habitats (two types of roads and urbanized areas) were joined into a single variable (anthropized areas).

We modelled foraging habitat selection by means of conditional logistic regression (Hosmer and Lemeshow 1989), which accounts for the intrinsically paired nature of the dataset. According to this approach, each set of foraging plots of a given breeding pair was matched to the respective control plots, henceforth taking into account the pair-based sampling design. Pair identity was thus specified as a so-called “stratum” variable. Study region was also tested as a random factor, but was subsequently discarded as no regional effect was found ( $P \sim 1$ ). Conditional logistic regressions were run by using the ‘clogit’ function of the ‘survival’ package in R (R Development Core Team, 2016).

Model selection was performed using an information-theoretic approach, based on the Akaike’s Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). First, the explanatory variables were divided in two groups, vegetation and other variables (Table 1), and tested for within-group collinearity by calculating the variance inflation factor (VIF) using the package car in R. For all variables within a given group, there were no collinearity issues ( $VIF < 3$  for all variables in both groups). Within each group, models with all possible variable combinations were constructed and models were ranked according to their AICc using the MuMIn package (Bartoń, 2016). The difference in AICc between each model and the top ranked model ( $\Delta AICc$ ) was calculated. Based on previous studies, we hypothesised that snowfinches would

preferentially forage in sites with high grass cover but low sward height (Brambilla et al., 2017b). Therefore, we added a potential interaction term to the vegetation group (grassland cover  $\times$  sward height in vegetation). Moreover, in order to test for selection of melting snow patch margins (see e.g. Antor, 1995) and on the basis of a preliminary data exploration (which suggested a potential curvilinear relationship for this factor), we also included a quadratic term for snow cover (in the other variables). Then, for each group we selected all the variables (and interactions) included in the most supported models ( $\Delta AICc < 2$ ) after the exclusion of ‘uninformative parameters’ (Arnold, 2010; Jedlikowski et al., 2016). We finally combined the retained variables of both groups and carried out a further model selection using the same procedure (see e.g. Assandri et al., 2016; Brambilla et al., 2016a). In the latter process, given that snowfinches could preferentially forage in fine-scaled mosaics of snow and grass (Brambilla et al., 2017b), we added an interaction term (snow  $\times$  grassland cover).

### **Past, current and future habitat suitability**

To predict climate-driven changes in foraging habitat suitability, we modelled snow cover and sward height as a function of season progression and environmental characteristics, selected on the basis of a potential effect of climate on those two variables according to literature and general knowledge. We built models based on the control plots, which were randomly selected and thus ensured unbiased sampling. First, we built a model relating snow cover to Julian date, solar radiation, elevation and slope. Then, we modelled sward height as a function of solar radiation, elevation, slope, snow cover and grazing occurrence, excluding the few sites without grass cover. In both cases, we used linear mixed models (LMM) fitted by means of maximum likelihood and considering breeding pair as a random factor to take into account the spatial dependency of sites frequented by the same breeding pair. We estimated past and simulated future conditions based on the observed rate of change in the date of snow melt: research from the Swiss Alps reported a linear pattern of advance in snow melt timing by c. 6 days per decade (5.8 days/decade; Klein et al.,

2016). To hindcast past conditions (40 years ago), we therefore decreased the sampling date by 24 days. To model conditions 50 years into the future (at year 2066), we added 30 days, assuming the trend in melting pattern will remain unaltered. We then recalculated predicted snow cover and grassland height for each of the three time steps (in the following termed ‘past’, ‘current’ and ‘future’).

Finally, we calculated for each plot (foraging or control,  $n = 470$ ) the potential suitability under past, current and future conditions, by means of the final habitat selection model obtained in the previous analysis, and averaged predicted habitat suitability for all plots related to each breeding pair. We used modelled snow cover and sward height (instead of the values actually recorded in the field) also for the current conditions in order to obtain habitat suitability estimates that were comparable with past and future conditions.

### **Mitigation scenarios**

To simulate and evaluate any potential benefits of targeted management actions to maintain foraging microhabitat suitability, we also modelled current and future suitability under two scenarios, with and without mitigation management. The ‘non-mitigation’ scenarios (without management) corresponded to the modelled habitat suitability as described above. For the mitigation scenarios (via habitat management), we assumed that sward height would be managed according to snowfinch optimal requirements by keeping grass height below 6 cm (see Fig. 2 and Brambilla et al., 2017b). We assumed that such optimal sward height could be achieved by mowing or controlled grazing. We therefore used the predicted sward height under current and future climate conditions, respectively, both adjusted by truncating the highest values at 6 cm. Finally, to evaluate whether habitat suitability significantly changed from past to current and from current to future conditions under both scenarios (with vs without management), we performed a Wilcoxon matched-pairs test on the mean plot suitability for each pair. For descriptive purposes, we also

counted the number of plots with average plot suitability above 0.5 (suitable plots) for each time step (past, current, and future).



## **Results**

### **Foraging habitat selection**

We obtained a single most supported synthetic model, as all other candidate models had a  $\Delta AICc > 2$ . According to this model, foraging habitat selection by breeding snowfinches was driven by negative effects of both sward height and anthropized areas, a quadratic effect of snow cover and a positive effect of grassland cover, all terms being statistically significant (Table 2). The influence of these predictors on the probability of occurrence of foraging snowfinches is shown graphically in Fig. 2.

### **Past, current and future habitat suitability**

The model for snow cover (intercept:  $-0.19 \pm 0.10$ ; coefficients for standardized predictors) suggested, as expected, a positive effect of elevation ( $0.24 \pm 0.11$ ) and negative effects of Julian date ( $-0.13 \pm 0.07$ ), slope ( $-0.05 \pm 0.09$ ) and solar radiation ( $-0.08 \pm 0.09$ ), and had a  $R^2$  equal to 0.17. The model for sward height (intercept:  $0.35 \pm 0.14$ ; coefficients for standardized predictors) revealed a positive effect of solar radiation ( $0.26 \pm 0.09$ ) and slope ( $0.47 \pm 0.09$ ): well exposed steep slopes are likely those where snow disappears earlier and where the plant growing season may be earlier, leading to higher swards. As expected, a negative effect on sward height was found for grazing (grazing occurrence:  $-0.08 \pm 0.15$ ), elevation ( $-0.60 \pm 0.14$ ) and snow cover ( $-0.14 \pm 0.08$ ), likely due to both different grass species at different elevations and to the delay in growing season caused by elevation and snow cover. The model for sward height had an  $R^2$  equal to 0.56.

Foraging habitat suitability was predicted to have declined from 1976 to 2016, and to continue declining from 2016 to 2066 at all breeding sites (Fig. 3). The predicted average site-level plot suitability had significantly declined from 1976 to 2016 (Wilcoxon matched pairs test,  $Z = -4.11$ ,  $p < 0.001$ ,  $n = 22$  breeding sites), and is expected to significantly decline further by 2066 ( $Z = -4.11$ ,  $p$

< 0.001). The overall number of suitable plots (plots with habitat suitability higher than 0.5;  $n = 470$ ) declined from 364 (77%) to 281 (60%) from 1976 to 2016 (-23% in the number of suitable plots), and was predicted to further decline to 191 (41%) by 2066 (i.e. a further change of -32% in the number of suitable plots relative to the current situation).

### **Mitigation scenarios**

The mitigation scenarios yielded higher current and future habitat suitability values than the estimates obtained without any intervention targeted at limiting sward height, especially for sites with most or some plots located at the lower end of the altitudinal range exploited by the species (Fig. 3). Under current conditions, if appropriate management actions were implemented, the number of suitable plots would be 359 (76%; which roughly corresponds to the figure back-projected to 1976 without management), while the average territory-level plot suitability would be significantly higher (+0.07; Wilcoxon matched pairs test;  $Z = -3.52$ ,  $p < 0.001$ ,  $n = 22$  breeding sites) compared to a scenario without management. The future number of suitable plots under an active mitigation scenario would be 268 (57%; very close to the number of currently suitable plots). Compared to a scenario with no management implemented in the future, average habitat suitability could thus be increased by 0.07 (Wilcoxon matched pairs test;  $Z = -3.52$ ,  $p < 0.001$ ,  $n = 22$  breeding sites) via mitigation measures.

## Discussion

Our retrospective and prospective modelling shows that a climate-sensitive species of high-Alpine ecosystems, the white-winged snowfinch, is put at risk by habitat loss induced by climate warming. Not only has it seemingly already lost a substantial fraction (-17% of plots, or -23% of suitable plots, from 1976) of its suitable habitat area in the Central European Alps over the past decades, but the unabated habitat alterations induced by climate change will also continue to reduce habitat suitability in the decades to come (-19%, or -32% of suitable plots, by 2066). To the best of our knowledge, this is the first study that has quantified species' fine-grained microhabitat requirements for reconstructing past, and constructing future, foraging habitat suitability in a high-elevation species, i.e. a species occurring in an ecosystem that is more affected by climate change than the global average (see Moritz and Agudo, 2013 and references therein). Indeed, most research on the impact of climate change on biodiversity has so far dealt with modelling macro-ecological relationships between climate and species' biological attributes (Bellard et al., 2012). This study is also one of the first to illustrate that mitigation measures (targeted sward management by grazing) could be implemented to maintain habitat suitability and thus buffer against the detrimental effects of climate change, in line with what Braunisch et al. (2014) have proposed for montane and subalpine forest bird species. This lack of fine-grained mechanistic studies of habitat selection is surprising as understanding species' ecological requirements is a prerequisite both for sound modelling of species-habitat relationships and for designing adequate mitigation strategies for conservation. In particular, microhabitat selection studies carried out during the main bottlenecks of a species' life cycle, notably the critical and intense phase of food provisioning to chicks, are key as breeding output depends on parental investment into progeny, which, in short-lived species such as the Snowfinch, drives demographic trajectories. The mechanical links evidenced in our field surveys between environmental characteristics favouring foraging activity (snow cover and sward height) and the alterations of these characteristics induced by climate warming exemplifies how

meaningful forecasting of future species distributions via spatial modelling should operate to gain predictive power.

### **Habitat suitability for foraging snowfinches is affected by climate-related habitat variables and anthropization**

Breeding snowfinches collected food for nestlings in microhabitats characterized by the intermediate snow cover intermixed with short grassland, while avoiding human-altered areas, notably roads and buildings. These results are in line with former findings obtained at a much coarser scale in a largely overlapping study area (Brambilla et al., 2017b). The preference for an intermediate snow cover (optimum at ca 40%) reflects species' foraging tactics: Snowfinches either collect invertebrate prey trapped on the snow surface (Antor, 1995), or exploit the margins of melting snow fields where tipulid larvae abound, one of their favourite prey (authors' personal observations). Sward height constrains foraging opportunities: short grass is likely to boost prey availability, which is prey abundance modified by its accessibility (Schaub et al., 2010). Yet, to further refine our mechanistic understanding of microhabitat-species associations, future work should also investigate how prey abundance varies with respect to snow cover and the melting front of the snow field.

Overall, our findings confirm that properly predicting mountain birds responses to global change necessitates the consideration of both climate and habitat factors simultaneously (Chamberlain et al., 2016). High-elevation species spend a large part of their life-cycle in extreme habitats. They have thus evolved specific adaptations to cope with harsh environmental conditions. However, climate change is accompanied by increased weather variability and an acceleration of extreme events, which represents a new evolutionary challenge for biodiversity in general (Di Marco and Santini, 2015) and high-alpine biodiversity in particular (Lu et al., 2009). Moreover, direct anthropogenic impacts on Alpine ecosystems are increasing: the tourism industry modifies

high-altitude landscapes and biodiversity via new infrastructure (e.g. Rolando et al., 2007), recreational disturbance (e.g. Arlettaz et al., 2015, 2013, 2007) and other anthropogenic stressors (Chamberlain et al., 2016). Although the snowfinch, a partly synanthropic bird, can benefit from human infrastructures both for nesting (mountain buildings, skilift-pylons and even nest-boxes) and winter foraging (seed-feeding stations at ski resorts or mountain chalets) (Cramp and Perrins, 1994), our results show that roads, paths, buildings and other man-made structures decrease foraging habitat quality during the reproductive period. It would thus be particularly interesting to estimate the year-round costs and benefits of breeding in anthropized vs natural conditions for snowfinches.

Climate change can threaten Alpine species to such an extent that the large-scale distribution of species like the snowfinch could shrink considerably (Brambilla et al., 2017a; Maggini et al., 2014). Our study demonstrates a high sensitivity of the snowfinch towards climate-induced alteration of microhabitat conditions, notably in snow cover and sward, shedding light on the possible mechanistic causes behind the ongoing range contraction of this and other cold-loving species (Scridel et al., 2017). Warming climate induces both an anticipation of the seasonal timing of snowmelt (Klein et al., 2016) and an earlier and faster grass growth at high elevations (Theurillat and Guisan, 2001), which affects the snowfinch as well as other elements of Alpine biocenoses (Pettorelli et al., 2007).

### **Buffering climate change impacts via habitat management**

While slowing down climate warming requires global measures to drastically reduce society's reliance on fossil energy sources, sward management through targeted grazing is amenable to local action. Our model outcomes suggest that the option to maintain sward height below ca 6 cm might offer some room to buffer the negative impacts of climate warming on foraging microhabitat configuration, especially for sites located at relatively low elevation, where grassland cover and sward height play a crucial role in determining habitat suitability for snowfinches. According to our

various scenarios, a systematic (i.e. unfortunately quite unlikely) implementation of that management option would have compensated for the decline in structural habitat suitability that has occurred from the 1970s and could also strongly reduce the predicted reduction of foraging habitat suitability over the next 50 years. However, it remains to be seen whether implementing this measure would suffice to compensate for the diminution of the area of suitable foraging habitat due to a thinner and earlier retreating snow pack. If the dependence on accessible foraging grounds is the main factor, then this might work. However, if the conditions prevailing along the melting snow front dictate not only prey accessibility, but also prey abundance, this measure will likely not suffice, unless the species can alter its breeding phenology towards earlier nesting. This emphasizes the need to better understand, first, how invertebrate prey availability (which is, again, abundance modified by accessibility) drives foraging microhabitat selection (Vickery and Arlettaz, 2012); and, second, what is the adaptive potential of the species to environmental change, notably in terms of reproductive phenology. From that viewpoint, the results of our retrospective habitat suitability model suggest that the snowfinch might have a limited capacity to cope with environmental change, notably with the ongoing major alterations in snow cover conditions. Investigations of its long-term breeding phenology are also needed to further appraise its adaptive potential. Finally, preventing the construction of new infrastructures at high elevation, converting disused tracks at construction sites into grassland, as well as ski-piste revegetation (Caprio et al., 2016) may limit or reduce further losses of suitable habitats due to human activities.

The present study highlights the importance of considering microhabitat selection for revealing fine-scale, functional and interacting effects of climate and land-use changes on climate-sensitive species and for identifying compensatory habitat management strategies that could to some extent allow buffering the negative effects of climate warming on high-Alpine biodiversity.

## **Acknowledgements**

We are very grateful to Parco Naturale Paneveggio-Pale di San Martino and to Parco Nazionale dello Stelvio for field assistance and facilities. PPPSM also provided financial support to D.S.'s PhD. E. Bassi, P. Partel, L. Pedrotti, P. Trotti provided helpful advices and support. We are grateful to the snowfinch European working group ([www.snowfinch.eu](http://www.snowfinch.eu)) for useful discussions on the species and to A. Barras, J. Besimo and C. Jourdan who helped with fieldwork in the Swiss Alps. Birds were handled with the permissions of the Swiss Office for the Environment.

**Table 1.** List of habitat variables measured within a 5-m radius at foraging and control plots, with information about methods, metrics and descriptor category. Ground cover variables sum up to 100%.

Variable type / variable name	Description	Unit	Group
<b>Vegetation structure</b>			
Sward height	5 measurements of grass height at the plot centre and at 2.5 m along each of the four cardinal directions (or at the closest point with grassland cover, respectively)	cm	Vegetation
<b>Ground cover</b>			
Grassland	cover of grassy vegetation	%	
Shrubs	dwarf-woody vegetation (e.g. <i>Rhododendron</i> , <i>Juniperus</i> , <i>Salix</i> ...)	%	
Snow	snow-covered areas	%	Other variables
Boulders	rocks detached from the substrate	%	
Bare ground	bare soil (compact soil)	%	
Rocks	emerging rocky substrate (bedrock)	%	
Scree	small rocky material (a few cm in diameter)	%	
Gravel roads	unpaved roads, large footpaths	%	
Paved roads	roads, paved parking	%	
Sand	sandy soil (not compact)	%	
Urbanized	buildings, walls, pylons	%	
Water	lakes, ponds, watercourses	%	
Other	other uncovered categories	%	
Pasture and/or presence of dung	dung of current or previous year or active grazing	yes / no	
<b>Topography</b>			
Slope	angle in degrees (°) calculated at the plot center using a digital elevation model (resolution: 1-5 m)	degree	
Solar radiation	calculated as global radiation for 21 <sup>st</sup> June based on a digital elevation model, incorporating the shadowing effect of the surrounding relief	kWh/m <sup>2</sup>	





**Table 2.** Best-fitting conditional logistic regression model for foraging habitat selection by breeding snowfinches during the nestling rearing period.

<b>Variable</b>	<b>Estimate (SE)</b>	<b>Z</b>	<b>P</b>
Grassland cover	0.57 (0.14)	4.14	< 0.001
Sward height	-0.85 (0.16)	5.37	< 0.001
Snow cover	2.00 (0.32)	6.18	< 0.001
Snow cover <sup>2</sup>	-0.72 (0.13)	5.32	0.003
Anthropized	-1.21 (0.45)	2.65	0.008

**Figure 1.** Map of the study area showing the 12 study sites monitored in the Swiss and Italian Alps. The location of some major towns (Bern, Chur, Milano and Trento) is also given for a better interpretation of the geographical extent of the study area. The inset shows the location of the study area (rectangle) within the European Alps (grey).

**Figure 2.** Habitat variables significantly (all  $P < 0.008$ ; see Table 2) affecting the probability that a bird foraged in a given habitat patch according to the best-fitting conditional logistic regression model reported in Table 2. In each panel, the variable's effects on predicted probability of habitat use (mean and 95% confidence interval) are shown while all other predictors included in the models are kept at their mean value.

**Figure 3.** Upper half: boxplots of past, current and future habitat suitability of all sampled plots (n=470) within each study area (n = 8 areas), according to the best-fitting model of microhabitat selection and the simulated scenarios of managed vs. unmanaged grassland sward height (in the managed scenario, grassland sward was kept at a maximum height of 6 cm; see Methods for details of the procedure). For each area, boxes show from left to right habitat suitability for different time steps and scenarios: past (black), current – unmanaged (white), current – management scenario (grey), future – unmanaged (white), future – management (grey). Plots show median, upper quartile, lower quartile, maximum and minimum values excluding outliers, i.e. value above 1.5 the upper quartile or below 1.5 the lower quartile.

Lower half: boxplot of plot (foraging and control) elevation within each study area.

## References

- Antor, R.J., 1995. The Importance of Arthropod Fallout on Snow Patches for the Foraging of High-Alpine Birds. *J. Avian Biol.* 26, 81–85. doi:10.2307/3677216
- Arlettaz, R., Nusslé, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P., Genoud, M., 2015. Disturbance of wildlife by outdoor winter recreation: Allostatic stress response and altered activity-energy budgets. *Ecol. Appl.* 25, 1197–1212. doi:10.1890/14-1141.1.sm
- Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., Jenni-Eiermann, S., 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proc. Biol. Sci.* 274, 1219–24. doi:10.1098/rspb.2006.0434
- Arlettaz, R., Patthey, P., Braunisch, V., 2013. Impacts of outdoor winter recreation on alpine wildlife and mitigation approaches: a case study of the black grouse. *impact Ski. Mt. Environnements* 137, 137–154.
- Arlettaz, R., Ruchet, C., Aeschimann, J., Brun, E., Genoud, M., Vogel, P., 2000. Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology* 81, 1004–1014. doi:10.1890/0012-9658(2000)081[1004:PTATDA]2.0.CO;2
- Arnold, T.W., 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *J. Wildl. Manage.* 74, 1175–1178. doi:10.1111/j.1937-2817.2010.tb01236.x
- Assandri, G., Bogliani, G., Pedrini, P., Brambilla, M., 2016. Diversity in the monotony? Habitat traits and management practices shape avian communities in intensive vineyards. *Agric. Ecosyst. Environ.* 223, 250–260. doi:10.1016/j.agee.2016.03.014
- Bartoń, K., 2016. MuMIn: Multi-Model Inference. R package version 1.15.6.
- Baudier, K.M., Mudd, A.E., Erickson, S.C., O'Donnell, S., 2015. Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). *J. Anim. Ecol.* 84, 1322–1330. doi:10.1111/1365-2656.12388
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. *Ecol. Lett.* 15, 365–377. doi:10.1111/j.1461-0248.2011.01736.x
- Bennett, N.L., Severns, P.M., Parmesan, C., Singer, M.C., 2015. Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos* 124, 41–53. doi:10.1111/oik.01490

- Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T., Schöner, W., 2001. Regional temperature variability in the European Alps: 1760-1998 from homogenized instrumental time series. *Int. J. Climatol.* 21, 1779–1801. doi:10.1002/joc.689
- Brambilla, M., Bergero, V., Bassi, E., Falco, R., 2015. Current and future effectiveness of Natura 2000 network in the central Alps for the conservation of mountain forest owl species in a warming climate. *Eur. J. Wildl. Res.* 61, 35–44. doi:10.1007/s10344-014-0864-6
- Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R., Bogliani, G., Pedrini, P., Rolando, A., Chamberlain, D., 2017a. A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. *Divers. Distrib.* 23, 727–738. doi:10.1111/ddi.12572
- Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P., Rubolini, D., 2017b. Foraging habitat selection by Alpine White-winged Snowfinches *Montifringilla nivalis* during the nestling rearing period. *J. Ornithol.* 158, 277–286. doi:10.1007/s10336-016-1392-9
- Brambilla, M., Gustin, M., Fulco, E., Celada, C., 2016a. Coarse landscape features predict occurrence, but habitat selection is driven by specific habitat traits: implications for the conservation of the threatened Woodchat Shrike *Lanius senator*. *Bird Conserv. Int.* 1–13. doi:10.1017/S0959270916000034
- Brambilla, M., Pedrini, P., Rolando, A., Chamberlain, D.E., 2016b. Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. *J. Biogeogr.* 43, 2299–2309. doi:10.1111/jbi.12796
- Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H., Bollmann, K., 2013. Selecting from correlated climate variables: A major source of uncertainty for predicting species distributions under climate change. *Ecography (Cop.)*. 36, 971–983. doi:10.1111/j.1600-0587.2013.00138.x
- Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., Bollmann, K., 2014. Temperate Mountain Forest Biodiversity under Climate Change: Compensating Negative Effects by Increasing Structural Complexity. *PLoS One* 9, e97718. doi:10.1371/journal.pone.0097718
- Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R., Schöner, W., 2009. Climate variability and change in the greater alpine region over the last two centuries based on multi-variable analysis. *Int. J. Climatol.* 29, 2197–2225. doi:10.1002/joc.1857
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*, Book. Springer, New York, NY. doi:10.1007/978-3-319-02868-2\_3

- Caprio, E., Chamberlain, D., Rolando, A., 2016. Ski-piste revegetation promotes partial bird community recovery in the European Alps. *Bird Study* 63, 470–478. doi:10.1080/00063657.2016.1216520
- Carnaval, A.C., Moritz, C., 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *J. Biogeogr.* 35, 1187–1201. doi:10.1111/j.1365-2699.2007.01870.x
- Catzefflis, F., 1975. Remarques sur la nidification rupestre de la Niverolle. *Nos Oiseaux* 33, 64–65.
- Chamberlain, D., Brambilla, M., Caprio, E., Pedrini, P., Rolando, A., 2016. Alpine bird distributions along elevation gradients: the consistency of climate and habitat effects across geographic regions. *Oecologia* 181, 1139–1150. doi:10.1007/s00442-016-3637-y
- Chamberlain, D.E., Negro, M., Caprio, E., Rolando, A., 2013. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biol. Conserv.* 167, 127–135. doi:10.1016/j.biocon.2013.07.036
- Chamberlain, D.E., Pedrini, P., Brambilla, M., Rolando, A., Girardello, M., 2016. Identifying key conservation threats to Alpine birds through expert knowledge. *PeerJ* 4, e1723. doi:10.7717/peerj.1723
- Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Laundre, J.A., 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology* 76, 694–711. doi:10.2307/1939337
- Chen, I., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species of climate warming. *Science* (80-. ). 333, 1024–1026. doi:10.1126/science.1206432
- Cramp, S., Perrins, C.M., 1994. *The birds of the Western Palearctic*, vol VIII. Oxford University Press, Oxford.
- Davies, Z.G., Wilson, R.J., Coles, S., Thomas, C.D., 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *J. Anim. Ecol.* 75, 247–256. doi:10.1111/j.1365-2656.2006.01044.x
- Di Marco, M., Santini, L., 2015. Human pressures predict species' geographic range size better than biological traits. *Glob. Chang. Biol.* 21. doi:10.1111/gcb.12834
- Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. *Glob. Chang. Biol.* 17, 990–996. doi:10.1111/j.1365-2486.2010.02266.x



- Fedy, B., Martin, K., 2011. The Influence of Fine-Scale Habitat Features on Regional Variation in Population Performance of Alpine White-Tailed Ptarmigan. *Condor* 113, 306–315. doi:10.1525/cond.2011.100070
- Fitzpatrick, M.C., Hargrove, W.W., 2009. The projection of species distribution models and the problem of non-analog climate. *Biodivers. Conserv.* 18, 2255–2261. doi:10.1007/s10531-009-9584-8
- Frey, S.J.K., Hadley, A.S., Betts, M.G., Robertson, M., 2016. Microclimate predicts within-season distribution dynamics of montane forest birds. *Divers. Distrib.* 22. doi:10.1111/ddi.12456
- Grangé, J.-L., 2008. Biologie de reproduction de la Niverolle Alpine *Montifringilla nivalis* dans le Pyrénées occidentales. *Nos Oiseaux* 55, 67–82.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. doi:10.1111/j.1461-0248.2005.00792.x
- Hanssen, S.A., Hasselquist, D., Folstad, I., Erikstad, K.E., 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings. Biol. Sci.* 272, 1039–46. doi:10.1098/rspb.2005.3057
- Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Chang. Biol.* 12, 2272–2281. doi:10.1111/j.1365-2486.2006.01256.x
- IPCC, 2013. Working Group I Contribution to the IPCC Fifth Assessment Report, Climate Change 2013: The Physical Science Basis, *Ippc*. doi:10.1017/CBO9781107415324.Summary
- Jedlikowski, J., Chibowski, P., Karasek, T., Brambilla, M., 2016. Multi-scale habitat selection in highly territorial bird species: Exploring the contribution of nest, territory and landscape levels to site choice in breeding rallids (Aves: Rallidae). *Acta Oecologica* 73, 10–20. doi:10.1016/j.actao.2016.02.003
- Johnson, R.E., 1968. Temperature regulation in the white-tailed ptarmigan, *Lagopus leucurus*. *Comp. Biochem. Physiol.* 24, 1003–1014. doi:10.1016/0010-406X(68)90813-X
- Klein, G., Vitasse, Y., Rixen, C., Marty, C., Rebetez, M., 2016. Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. *Clim. Change* 139, 637–649. doi:10.1007/s10584-016-1806-y
- Körner, C., Ohsawa, M., 2006. Mountain systems, in: Hassan, R., Scholes, R., Ash, N. (Eds.), *Ecosystem and Human Well-Being: Current State and Trends*. Island Press, Washington, pp. 681–716.

- La Sorte, F.A., Jetz, W., 2010. Projected range contractions of montane biodiversity under global warming. *Proc. Biol. Sci.* 277. doi:10.1098/rspb.2010.0612
- Lagerholm, V.K., Sandoval-Castellanos, E., Vaniscotte, A., Potapova, O.R., Tomek, T., Bochenski, Z.M., Shepherd, P., Barton, N., Van Dyck, Marie-C., Miller, R., Höglund, Jacob, Yoccoz, N.G., Dalén, L., Stewart, J.R., 2017. Range shifts or extinction? Ancient DNA and distribution modelling reveal past and future responses to climate warming in cold-adapted birds. *Glob. Chang. Biol.* 23, 1425–1435. doi:10.1111/gcb.13522
- Lu, X., Ke, D.H., Zeng, X.H., Yu, T.L., 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. *J. Arid Environ.* 73, 1103–1108. doi:10.1016/j.jaridenv.2009.06.011
- Maggini, R., Lehmann, A., Zbinden, N., Zimmermann, N.E., Bolliger, J., Schröder, B., Foppen, R., Schmid, H., Beniston, M., Jenni, L., 2014. Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds. *Divers. Distrib.* 20, 708–719. doi:10.1111/ddi.12207
- Martínez-Miranzo, B., Banda, E.I., Aguirre, J.I., 2016. Multiscale analysis of habitat selection by Bonelli's eagle (*Aquila fasciata*) in NE Spain. *Eur. J. Wildl. Res.* 62, 673–679. doi:10.1007/s10344-016-1041-x
- Moritz, C., Agudo, R., 2013. The Future of Species Under Climate Change: Resilience or Decline? *Science* (80-. ). 341, 504–508. doi:10.1126/science.1237190
- Naef-Daenzer, B., Widmer, F., Nuber, M., 2001. A test for effects of radio-tagging on survival and movements of small birds. *Avian Sci.* 1, 15–23.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42. doi:10.1038/nature01286
- Pernollet, C.A., Korner-Nievergelt, F., Jenni, L., 2015. Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis* (Lond. 1859). 157, 823–836. doi:10.1111/ibi.12298
- Pettorelli, N., Pelletier, F., Von Hardenberg, A., Festa-Bianchet, M., C??t??, S.D., 2007. Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. *Ecology* 88, 381–390. doi:10.1890/06-0875
- Pincebourde, S., Murdock, C.C., Vickers, M., Sears, M.W., 2016. Fine-scale microclimatic variation can shape the responses of organisms to global change in both natural and urban environments, in: *Integrative and Comparative Biology*. Oxford University Press, pp. 45–61. doi:10.1093/icb/icw016

- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* (80-. ). 315, 95–97. doi:10.1126/science.1135471
- Pradervand, J.-N., Dubuis, A., Pellissier, L., Guisan, A., Randin, C., 2014. Very high resolution environmental predictors in species distribution models: Moving beyond topography? *Prog. Phys. Geogr.* 38, 79–96. doi:10.1177/0309133313512667
- R Development Core Team, 2016. A Language and Environment for Statistical Computing.
- Rappole, J.H., Tipton, A.R., 1991. New harness design for attachment of radio transmitters to small passerines (Nuevo Diseño de Arnés para Atar Transmisores a Passeriformes Pequeños). *J. F. Ornithol.* 62, 335–337.
- Rauter, C.M., Reyer, H.-U., Bollmann, K., 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the Water Pipit *Anthus spinoletta*. *Ibis* (Lond. 1859). 144, 433–444. doi:10.1046/j.1474-919X.2002.00013.x
- Rolando, A., Caprio, E., Rinaldi, E., Ellena, I., 2007. The impact of high-altitude ski-runs on alpine grassland bird communities. *J. Appl. Ecol.* 44, 210–219. doi:10.1111/j.1365-2664.2006.01253.x
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., Imeson, A., 2008. Attributing physical and biological impacts to anthropogenic climate change. *Nature* 453, 353–357. doi:10.1038/nature06937
- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L., Arlettaz, R., 2010. Patches of Bare Ground as a Staple Commodity for Declining Ground-Foraging Insectivorous Farmland Birds. *PLoS One* 5, e13115. doi:10.1371/journal.pone.0013115
- Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. *Glob. Chang. Biol.* 20, 495–503. doi:10.1111/gcb.12439
- Schiel, D.R., Steinbeck, J.R., Foster, M.S., 2004. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85, 1833–1839. doi:10.1890/03-3107
- Scridel, D., Bogliani, G., Pedrini, P., Iemma, A., Hardenberg, A. von, Brambilla, M., 2017. Thermal niche predicts recent changes in range size for bird species. *Clim. Res.* 73, 207–216. doi:10.3354/cr01477

- Sekercioglu, C.H., Schneider, S.H., Fay, J.P., Loarie, S.R., 2008. Climate change, elevational range shifts, and bird extinctions. *Conserv. Biol.* 22, 140–150. doi:10.1111/j.1523-1739.2007.00852.x
- Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., Bishop, P.J., Corn, P.S., Dovey, L., Griffiths, R.A., Lowe, K., Mahony, M., McCallum, H., Shuker, J.D., Simpkins, C., Skerratt, L.F., Williams, S.E., Hero, J.-M., 2011. Engineering a future for amphibians under climate change. *J. Appl. Ecol.* 48, 487–492. doi:10.1111/j.1365-2664.2010.01942.x
- Strinella, E., Ricci, F., Vianale, P., 2007. Uso dell'habitat nel Fringuello alpino (*Montifringilla nivalis*) in periodo riproduttivo in un'area sub-antropizzata: Campo Imperatore (Gran Sasso-Abruzzo). *Alula* 14, 107–114.
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B., Thomas, C.D., 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120, 1–8. doi:10.1111/j.1600-0706.2010.18270.x
- Theurillat, J.-P., Guisan, A., 2001. Potential Impact of Climate Change on Vegetation in the European Alps: A Review. *Clim. Change* 50, 77–109. doi:10.1023/A:1010632015572
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–8. doi:10.1038/nature02121
- Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C., Beissinger, S.R., 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Glob. Chang. Biol.* 18, 3279–3290. doi:10.1111/j.1365-2486.2012.02784.x
- Townsend, J.M., Rimmer, C.C., McFarland, K.P., 2012. Radio-transmitters do not affect seasonal mass change or annual survival of wintering Bicknell's Thrushes. *J. F. Ornithol.* 83, 295–301. doi:10.1111/j.1557-9263.2012.00378.x
- Turlure, C., Choutt, J., Baguette, M., Van Dyck, H.A.N.S., 2010. Microclimatic buffering and resource-based habitat in a glacial relict butterfly: Significance for conservation under climate change. *Glob. Chang. Biol.* 16, 1883–1893. doi:10.1111/j.1365-2486.2009.02133.x
- Vickery, J., Arlettaz, R., 2012. The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes, in: *Birds and Habitat: Relationships in Changing Landscapes*. pp. 177–204.

Visinoni, L., Pernollet, C.A., Desmet, J.-F., Korner-Nievergelt, F., Jenni, L., 2015. Microclimate and microhabitat selection by the Alpine Rock Ptarmigan (*Lagopus muta helvetica*) during summer. *J. Ornithol.* 156, 407–417. doi:10.1007/s10336-014-1138-5

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5, 475–482. doi:10.1890/070037

Fig. 1.

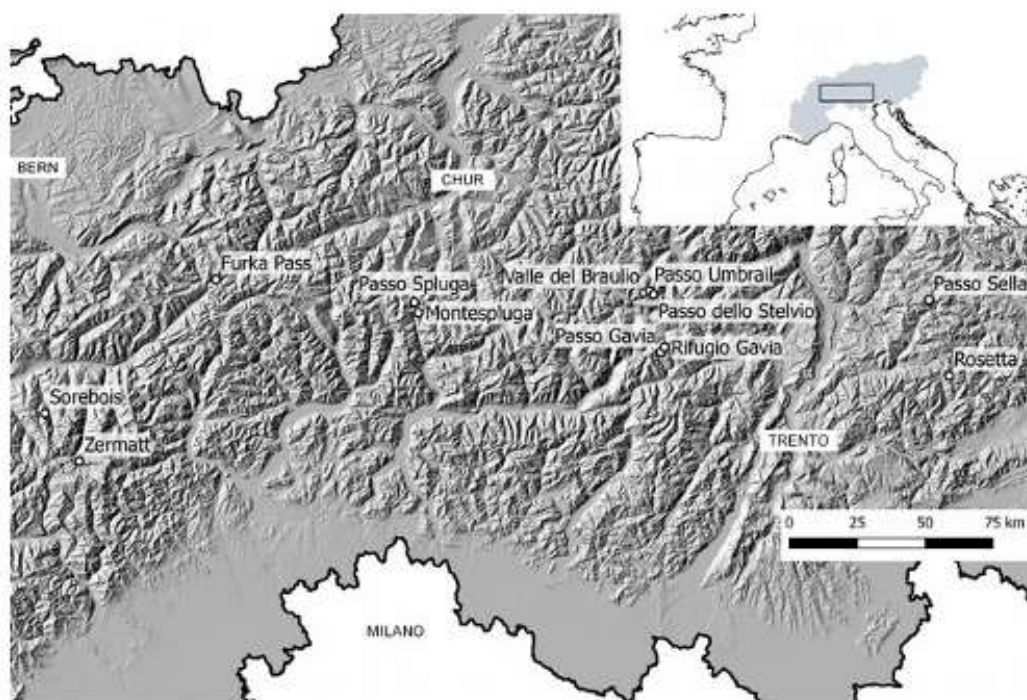


Fig. 2.

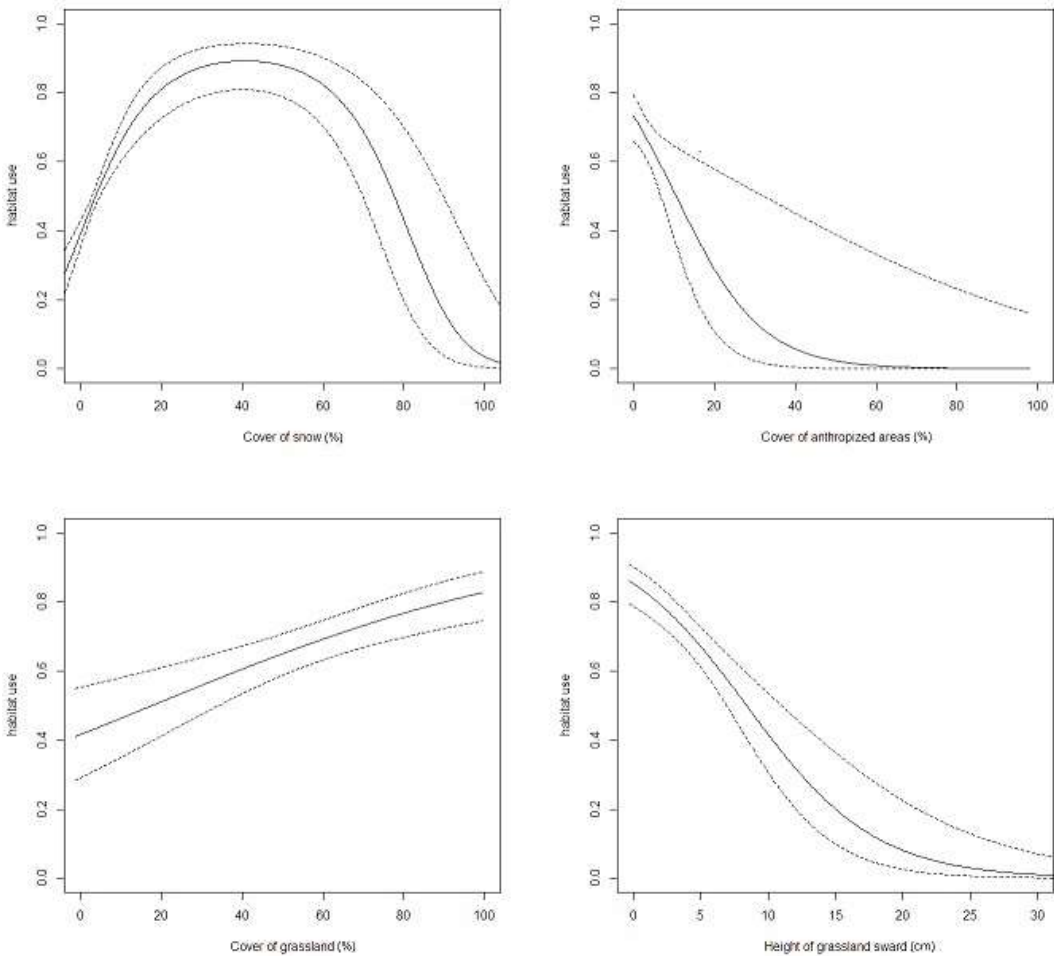


Fig. 3.

